

Prey Selection by Five Species of Vespertilionid Bats on Sapelo Island, Georgia

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ABSTRACT. -- Prey items obtained from fecal samples of 132 individuals representing five species of vespertilionid bats were compared to available prey as determined by insect light trapping in foraging habitats on Sapelo Island, Georgia. Four orders of insects dominated the diet of these bats: Coleoptera, Hymenoptera, Lepidoptera, and Hemiptera. Homoptera and Diptera were present in smaller proportions. All five bat species exhibited significant selection for or against certain insect orders. The evening bat (*Nycticeius humeralis*) consumed Coleoptera and Hymenoptera in proportion to their availability, but significantly fewer Homoptera than were available in the foraging habitats. Differences in feeding selectivity were observed between sexes and age groups. Adult male and juvenile evening bats consumed significantly fewer Coleoptera and more Hymenoptera than were available in the foraging habitats; adult females showed little feeding selectivity. The Seminole bat (*Lasiurus seminolus*) consumed Homoptera and Diptera in significantly lower proportion to their availability. The eastern pipistrelle (*Pipistrellus subflavus*) consumed significantly more Lepidoptera and fewer Coleoptera and Homoptera in proportion to their availability. The big brown bat (*Eptesicus fuscus*) fed mostly on Coleoptera and Lepidoptera, whereas the northern yellow bat (*L. intermedius*) consumed only Coleoptera and Hymenoptera.

Twelve species of bats occur in Lower Coastal Plain ecosystems of South Carolina, Georgia, and northern Florida (Barbour and Davis 1969, Hall 1981). With the exception of Zinn and Humphrey's (1981) study of prey availability and prey selection of the southeastern bat, *Myotis austroriparius* (Rhoads 1897), only anecdotal comments regarding foraging behavior of bats inhabiting

these regional ecosystems are available (Harper 1927, Sherman 1935, 1939, Moore 1949, Ivey 1959, Golley 1962, 1966, Neuhauser and Baker 1974, Sanders 1978, Schacher and Pelton 1979).

In conjunction with mist netting studies relating to roost site selection and habitat use of bats on Sapelo Island, Georgia (Menzel et al. 1995), we undertook a comparative study of prey selection based on analysis of fecal pellet contents collected from five species of bats captured on the island: evening bat, *Nycticeius humeralis* (Rafinesque 1818), Seminole bat, *Lasiurus seminolus* (Rhoads 1895), eastern pipistrelle, *Pipistrellus subflavus* (Cuvier 1832), northern yellow bat, *L. intermedius* Allen 1862, and big brown bat, *Eptesicus fuscus* (Beauvois 1796). To determine the degree of prey selectivity by the bats from among potential prey, we compared fecal pellet contents to available insects collected at vegetational community types on the island where bats foraged.

STUDY AREA

The study was conducted on Sapelo Island, McIntosh County, Georgia from 19 June through 24 July 1995. Sapelo Island is located approximately 63 km south of Savannah and 5.5 km off shore (31°27'N, 81°16'W). The island is approximately 16 by 3.2 km in size and is typical of barrier islands of the southeastern Atlantic Bight (Johnson et al. 1974). Seven well-defined vegetational community types characteristic of regional lower Coastal Plain ecosystems are present on the island (Shaw and Fredine 1956). Bats are known to forage in all seven of these communities. Longleaf pine stands (*Pinus palustris*) are restricted to the northern third of the island. The remaining vegetational community types are located throughout and include stands of pond pine (*P. serotina*), loblolly-slash pine (*P. taeda* and *P. elliotii*), mixed pine-oak (upland oaks comprise less than 25 % of the overstory), mixed oak-pine (pines comprise less than 25 % of the overstory), oak stands dominated by live oak (*Quercus virginiana*), and high marsh. Further descriptions of the floral associates of these vegetational communities are provided by Johnson et al. (1974).

The climate of Sapelo Island is characterized by long, warm summers and short, mild winters. Average temperatures for June and July are 26.3 and 27.7 C, respectively. Average monthly rainfall for June and July is 14.58 and 15.65 cm, respectively (National Climatic Center 1983, Johnson et al. 1974).

METHODS

Capture Techniques - Bats were captured throughout the study using 3 x 12 m mist nets set over or near ponds in all seven major vegetational community types on the island. Nets were opened from dusk until 0200 hours. Bats are known to forage over dunes, marshes, and open salt water. However, no effort was made to mist net in these areas. Bats netted throughout the night were held in a 32-ounce cup, and fecal pellets were collected. All bats were released

within an hour, whether fecal pellets were collected or not. Data recorded from bats included species, sex, and age class (juvenile or adult). Age classes were determined by back-lighting finger joints to examine the level of epiphyseal diaphyseal fusion (Anthony 1988).

Insect Sampling - A variety of methods are available to sample insects. All of these have inherent biases (Kunz 1988). While light traps are biased toward phototrophic insects (Bowden 1982), they have been shown to be satisfactory in foraging studies of bats (Taylor and Carter 1961, Brack and LaVal 1985, Jones 1990, Lacki et al. 1995).

Seven, 10-watt, black light insect traps were powered by automotive batteries. One was placed in each vegetational community type. Traps were suspended from 1 to 3 m above the ground and positioned to be visible from most points within a 60-m radius. Traps were operated each night between 2100 and 0300 hours at the same time bats were tracked using telemetry. Insects were removed each night and frozen for subsequent identification. The size of the insects considered to be consumable ranged from 2 to 25 mm for all bats (Gould 1955, Ross 1961, Black 1974, Feldhamer et al. 1995). A total of 8,753 insects in this size range was identified to order, and proportions of orders present were calculated. Regression analysis indicated no changes in relative insect abundance in the respective habitat types over our sampling period. Therefore, we combined data for insects in each habitat type over our sampling period.

Fecal Analysis - Fecal samples were placed in a petri dish with 70% ethanol solution and teased apart using probes and forceps (Whitaker 1988). All fecal pellets collected from a single individual were examined together using a dissecting microscope. To eliminate researcher bias, fecal samples were examined using identification numbers that were referenced to the species, age, and sex of the bats. A reference collection of insects collected during the study was used to help identify fecal matter (Whitaker 1988). Most insects were identified to order, some to family or species. Percent volume of prey taxa was visually estimated for each sample, and percent occurrence was calculated. Lepidopterans were often only represented in fecal samples by scales. Therefore, percent volume of this order was estimated using a modified version of Black's method (1972), and were not considered if present in small numbers.

Selectivity - Whitaker (1994) noted that to distinguish between opportunistic versus selective feeding by insectivorous bats, it is necessary to assess the insect taxa available to the bats and compare these to prey items actually eaten. We followed Whitaker (1994) in assessing prey taxa availability by sampling insects in the habitats in which the bats were foraging (see below). We then compared prey taxa availability in different habitats to the insect taxa found in

the fecal pellets. If prey availability at sampling sites differed significantly from prey taxa obtained in fecal samples, we assumed the bats were feeding selectively.

One-way analysis-of-variance (ANOVA) and the Bonferonni multiple range test revealed that the diet of the bats remained constant over our sampling period. Therefore, we compared the fecal samples of each species of bat to the samples of insects collected throughout the summer.

Since it is likely that bats feed in more than one vegetational community type and the proportion of available prey may differ between vegetational community types, we again followed Whitaker (1994) by prorating the time spent foraging in different vegetational community types. We used telemetry data to determine the time each bat species spent in each vegetational community type and multiplied this by the proportion of insect taxa collected in that vegetational community type. The prorated time spent in each vegetational community type was then summed to obtain the total proportion of insect taxa in the bat's hypothetical foraging area. Only fecal samples from bats captured while foraging in areas where insects were collected were used in this analysis. Differences between expected and actual diet were determined using an ANOVA (Sokal and Rohlf 1987). Significance was accepted at the $p < 0.05$ level.

RESULTS AND DISCUSSION

Fecal samples from 132 individual bats were examined: 99 *N. humeralis* (Table 1), 24 *L. seminolus*, 4 *P. subflavus*, 3 *E. fuscus*, 2 *L. intermedius* (Tables 2). Due to the large sample size of *N. humeralis*, we were also able to analyze this species in three groups: adult males, adult females, and juveniles. Table 1 and 2 summarize fecal analysis data and prey availability comparisons. Samples were collected from bats netted in all vegetational community types except pine-oak, a community in which no bats were captured. Due to the size of insect fragments found in fecal pellets, identification of only six major orders was possible: Coleoptera, Hymenoptera, Lepidoptera, Hemiptera, Homoptera, and Diptera. Other orders may have been present in lower quantities. Percent volume and percent occurrence of insect orders consumed varied among species (Tables 1 and 2). While previous studies suggest that small, insectivorous bats are opportunistic feeders (Kunz 1974, Fenton and Morris 1976, Swift et al. 1985), each of the five species we studied demonstrated statistically significant feeding selectivity for certain insect orders.

Nycticeius humeralis

Fecal samples from 99 evening bats were examined (Table 1). Six orders of prey items were found. Coleoptera were present in 91% of the fecal samples followed by Hymenoptera (69%), Lepidoptera (48.5%), Hemiptera (40.5%), Homoptera (7%), and Diptera (8%). No significant depar-

Table 1.--Percent occurrence (Fec. Occ.), and total volume (Fec. Vol.) of insect taxa recovered from fecal samples of *N. humeralis*, compared with percentage available (Hab. Avl.) in foraging habitats on Sapelo Island, Georgia.

	<i>N. humeralis</i> (n = 99)						Adult Male (n = 16)						Adult Female (n = 41)						Juvenile (n = 42)					
	% Occ.	% Fec. Vol.	% Hab. Avl.	% Occ.	% Fec. Vol.	% Hab. Avl.	% Occ.	% Fec. Vol.	% Hab. Avl.	% Occ.	% Fec. Vol.	% Hab. Avl.	% Occ.	% Fec. Vol.	% Hab. Avl.	% Occ.	% Fec. Vol.	% Hab. Avl.	% Occ.	% Fec. Vol.	% Hab. Avl.	% Occ.	% Fec. Vol.	% Hab. Avl.
Coleoptera	91	45	75	87.5	28.5*	75	93	53.5	75	90	43	75	90	43	75	90	43	75	90	43	75	90	43	75
Hymenoptera	69	36	3.5	81	47.5	3.5	58.5	26.5	3.5	74	40.5	3.5	58.5	26.5	3.5	74	40.5	3.5	58.5	26.5	3.5	74	40.5	3.5
Lepidoptera	48.5	7	10	62.5	10	10	40	6.5	10	52	5.5	10	40	6.5	10	52	5.5	10	40	6.5	10	52	5.5	10
Hemiptera	40.5	11	2	44	11.5	2	46	12	2	33	10	2	46	12	2	33	10	2	46	12	2	33	10	2
Homoptera	7	.03	8	6	0*	8	10	.5*	8	5	0*	8	10	.5*	8	5	0*	8	10	.5*	8	5	0*	8
Diptera	8	.07	1	12.5	2	1	12	1	1	2	0*	1	12	1	1	2	0*	1	12	1	1	2	0*	1

Differences between fecal samples and available samples

* Significant differences ($P < 0.05$).

Table 2.--Percent occurrence (Fec. Occ.), and total volume (Fec. Vol.) of insect taxa recovered from fecal samples of four species of bats, compared with percentage available (Hab. Avl.) in foraging habitats on Sapelo Island, Georgia.

	<i>L. seminolus</i> (n = 24)			<i>P. subflavus</i> (n = 4)			<i>E. fuscus</i> (n = 3)			<i>L. intermedius</i> (n = 2)		
	% Fec. Occ.	% Fec. Vol.	% Hab. Avl.	% Fec. Occ.	% Fec. Vol.	% Hab. Avl.	% Fec. Occ.	% Fec. Vol.	% Hab. Avl.	% Fec. Occ.	% Fec. Vol.	% Hab. Avl.
Coleoptera	92	49.5	76	25	6*	66	100	78	74	100	31	66
Hymenoptera	50	20	3	50	4	12	0	0*	7	100	69	12
Lepidoptera	71	25	11	100	74*	5	100	21	5	0	0*	5
Hemiptera	25	5	2	25	12	3	0	0*	2	0	0	3
Homoptera	4	.3*	7	0	0*	12	0	0*	9	0	0*	12
Diptera	4	.2*	1	25	4	2	33.3	1	2	0	0	2

Differences between fecal samples and available samples

* Significant differences ($P < 0.05$).

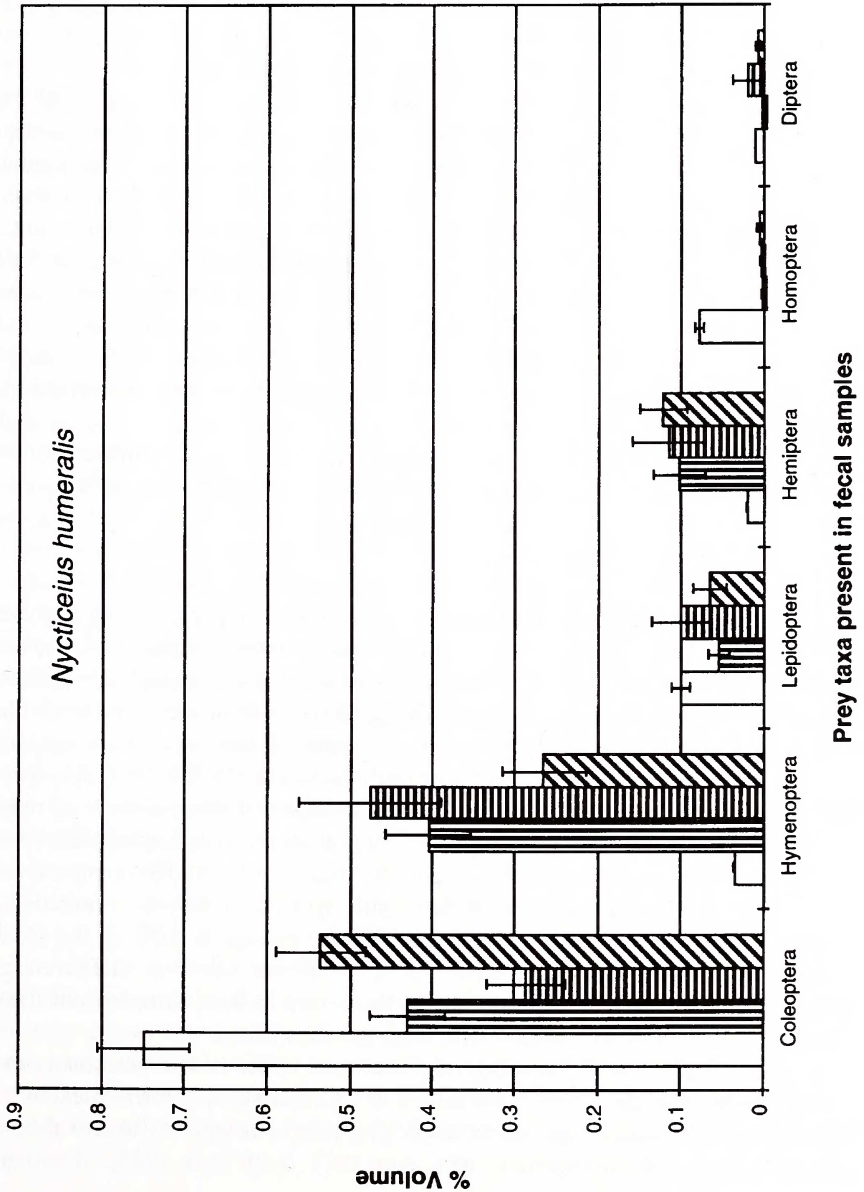
tures between fecal volume and prey availability were noted except that Homoptera occurred in significantly lower volume ($p < 0.001$) in fecal samples than were available in the environment. The relatively large number of evening bats netted allows for a comparison between adult males ($n = 16$), adult females ($n = 41$), and juveniles ($n=42$) of the percent volume of insect taxa in fecal samples to the percent availability in environment (Table 1).

Regardless of sex and age, the fecal volume of evening bats was composed primarily of Coleoptera, Hymenoptera, and Hemiptera (combined these groups comprised 88% or more of the diet). Adult males consumed significantly fewer Coleoptera ($p = 0.001$) and Homoptera ($p < 0.001$) than were available in the environment (Table 1). The large proportion of Hymenoptera in fecal samples of males compared to availability was not significant ($p = 0.071$), but suggests a feeding preference. Adult males consumed smaller proportions of Lepidoptera, Hemiptera, and Diptera than did males or juveniles. Combined, these taxa constituted only 23.5 % of the diet and were consumed in roughly equivalent proportion to their availability in the environment (21%). Adult females showed little feeding selectivity. Homoptera differed significantly ($p = 0.004$) between the percent volume in the fecal samples and their availability in the environment. However, these comprised only a very small portion (0.5 %) of the diet. The taxa comprising over 99.5% of the fecal contents were consumed in equal proportion to their availability in the environment. Juvenile evening bats consumed similar prey to that of adult males and females. However, their prey consisted of significantly fewer Coleoptera ($p = 0.056$), Homoptera ($p < 0.001$), and Diptera ($p < 0.001$) than were available in their environment.

Significant differences in fecal volume of prey species were observed between adult male and female evening bats. Male evening bats consumed significantly fewer Coleoptera ($p = 0.025$) than females and also significantly fewer than in proportion to their availability (Table 1, Figure 1). Males also consumed significantly more Hymenoptera ($p = 0.039$) than females, and in significantly higher proportion to their availability. This might be related to differences in the physiological state and metabolic requirements of males and females during the time of the year of our study (e.g., parturition and lactation). Adult females are expected to be under high levels of nutritional stress and coupled with time constraints imposed by offspring, might not be able to be as selective in their diets as adult males. Juveniles are not as constrained by time or energy as they are by their lack of foraging experience. Juveniles may be less selective, eating whatever they can catch. Adult males are not restricted by time constraints, experience or energy demands, allowing them more dietary selectivity.

A few reports on the foraging habits of the evening bat are available (Ross 1967 in Freeman 1981, Whitaker 1972, Zinn 1977, Whitaker and Clem 1992, Feldhamer et al. 1995). Most of these studies had small sample sizes, and none compared diet to relative prey abundance. Coleoptera were generally

Fig. 1. Comparison of available insect sample percentages (white) with fecal analysis from juvenile (vertical bars), adult male (horizontal bars), and adult female (diagonal bars) *Nycticeius humeralis* captured between 19 June and 24 July 1995, on Sapelo Island, Georgia.



reported to be the most important food source. Although we found Coleoptera to be present in 91% of the fecal samples, we found that significantly fewer Coleoptera were fed upon by adult males and juveniles than were available in environment. Zinn (1977) and Ross (1967 in Freeman 1981) also reported Hymenoptera from fecal pellets of the evening bat. We also found Hymenoptera (mostly flying ants -- Formicidae) to be a major food source.

Lasiurus seminolus

Six orders of prey items were also found in the fecal samples of 24 Seminole bats (Table 2). In fecal samples of Seminole bats 94.5% of the diet was from three orders: Coleoptera, Hymenoptera, and Lepidoptera. The percent volume of these taxa in fecal samples was not significantly different from their availability in the environment. Smaller proportions of Hemiptera, Homoptera, and Diptera (combined, constituting only 5.5% of the diet) were also found. Percent volumes of Homoptera ($p < 0.001$) and Diptera ($p < 0.001$) in the fecal samples were significantly lower than the percent available in the environment. There have been two reports of this species gleaning (Sherman 1935, Barbour and Davis 1969). Sherman (1939) found Coleoptera, Homoptera, and Diptera in the contents of a single stomach. Zinn (1977) found Coleoptera, Odonata, and Hymenoptera to be food items. These observations combined with our results confirm the importance of Coleoptera and Hymenoptera in the diet of Seminole bats.

Pipistrellus subflavus

The fecal samples obtained from four eastern pipistrelles suggest the most dramatic foraging selectivity of the five species of bats studied. Five taxonomic orders were present in fecal samples (Table 2). Lepidoptera were present in 100% of the fecal samples. They constituted only 5% of prey taxa available in the environment, but made up 74% of the volume of prey items in fecal samples. Coleoptera, on the other hand, were present in only 25% of the fecal samples. They constituted 66% of taxa available in environment, but made up only 6% of the volume in the fecal samples. Differences for both Lepidoptera ($p = 0.007$) and Coleoptera ($p < 0.001$) were highly significant. No Homoptera were found in the fecal samples, although they made up 12% of the prey available in the environment ($p < 0.001$). Hymenoptera were present in 50% of the fecal samples, and Hemiptera and Diptera in 25% of the samples. Differences between the respective percent volume of these taxa in fecal samples and their percent availability in the environment were not significant.

Whitaker (1972) found that the 23 eastern pipistrelles he examined consumed nearly 30% Coleoptera and only 7.3% Lepidoptera. Other researchers have found Coleopterans present in lower proportions or entirely absent (Sherman 1939, Ross 1967 in Freeman 1981, Zinn 1977, Swift et al. 1985). Sherman

(1939) and Swift et al. (1985) both reported Diptera to be the most important food source for the eastern pipistrelle.

Eptesicus fuscus

Three taxonomic orders of prey were observed in the fecal samples of three big brown bats. Coleoptera and Lepidoptera were found in 100% of the fecal samples, whereas Diptera was only observed in one (Table 2). The diet of these bats was dominated by Coleoptera (78%). Beetles were fed upon in proportions equal to their availability. Lepidoptera appeared to be selectively fed upon. They comprised 21% of the fecal volume, compared to 5% of available insects sampled in the environment ($p = 0.056$). The small proportion of Diptera observed in fecal samples was not significantly different from their availability. Hymenoptera, Hemiptera, or Homoptera were not observed in the fecal samples. The diet of the bats we examined was similar to that reported in previous studies, in that Coleoptera predominated in the diet (Hamilton 1933, Phillips 1966, Ross 1967 in Freeman 1981, Whitaker 1972, Whitaker 1995). Whitaker (1972) found that 4.3% of the diet was composed of non-flying insects, suggesting that big brown bats may occasionally glean from the ground or foliage.

Lasiurus intermedius

The fecal samples of the two northern yellow bats captured were composed entirely of Coleoptera and Hymenoptera (Table 2). Coleoptera and Hymenoptera made up 31% and 69% of the fecal samples by volume, respectively. No significant difference between percent fecal volume and percent availability was observed for Coleoptera. However, differences between fecal volume and availability of Hymenoptera approached significance ($p = 0.067$), suggesting a feeding preference for this taxa.

Previous studies reported Coleoptera as the most frequently consumed prey taxa (Sherman 1939, Zinn 1977). Hymenoptera were also found in lower volumes. Ivey (1959) reported observing northern yellow bats foraging in back dune depressions where mosquitoes and flies were abundant. However, in contrast to Webster et al. (1980), he did not actually witness bats consuming these insects.

CONCLUSION

Despite small sample sizes, we found significant differences among available and consumed prey in all five species of bats studied. Although there are some biases associated with any type of sampling (Taylor and Carter 1961, Rabinowitz and Tuttle 1982); the comparison of the available prey and prey that represented in the fecal samples gives us a greater insight into the complex foraging habits of some of the bat species found in the Southeast.

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